Can sea urchins beat the heat? Sea urchins, thermal tolerance and climate change

Elizabeth Sherman

The massive die-off of the long-spined sea urchin, *Diadema antillarum*, a significant reef grazer, in the mid 1980s was followed by phase shifts from coral dominated to macroalgae dominated reefs in the Caribbean. While *Diadema* populations have recovered in some reefs with concomitant increases in coral cover, the additional threat of increasing temperatures due to global climate change has not been investigated in adult sea urchins. In this study, I measured acute thermal tolerance of *D. antillarum* and that of a sympatric sea urchin not associated with coral cover, *Echinometra lucunter*, over winter, spring, and summer, thus exposing them to substantial natural thermal variation. Animals were taken from the wild and placed in laboratory tanks in room temperature water (~22°C) that was then heated at 0.16-0.3 °C min^{-1} and the righting behavior of individual sea urchins was recorded. I measured both the temperature at which the animal could no longer right itself (T_{LoR}) and the righting time at temperatures below the T_{LoR}. In all seasons, *D. antillarum* exhibited a higher mean T_{LoR} than *E. lucunter*. The mean T_{LoR} of each species increased with increasing environmental temperature revealing that both species acclimatize to seasonal changes in temperatures. The righting times of *D. antillarum* were much shorter than those of *E. lucunter*. The longer relative spine length of *Diadema* compared to that of *Echinometra* may contribute to their shorter righting times, but does not explain their higher T_{LoR}. The thermal safety margin (the difference between the mean collection temperature and the mean T_{LoR}) was between 3.07-3.66°C for *Echinometra* and 3.79-5.67°C for *Diadema*. While these thermal safety margins exceed present day temperatures, they are modest compared to those of temperate marine invertebrates. If sea temperatures increase more rapidly than can be accommodated by the sea urchins (either by genetic adaptation, phenotypic plasticity, or both), this will have important consequences for the structure of coral reefs .

2   **Can sea urchins beat the heat? Sea urchins, thermal tolerance and climate change.**

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9   **ABSTRACT**

10   The massive die-off of the long-spined sea urchin, *Diadema antillarum*, a significant reef grazer,

11   in the mid 1980s was followed by phase shifts from coral dominated to macroalgae dominated

12   reefs in the Caribbean. While *Diadema* populations have recovered in some reefs with

13   concomitant increases in coral cover, the additional threat of increasing temperatures due to

14   global climate change has not been investigated in adult sea urchins. In this study, I measured

15   acute thermal tolerance of *D. antillarum* and that of a sympatric sea urchin not associated with

16   coral cover, *Echinometra lucunter*, over winter, spring, and summer, thus exposing them to

17   substantial natural thermal variation. Animals were taken from the wild and placed in laboratory

18   tanks in room temperature water (~22°C) that was then heated at 0.16-0.3 °C min^{-1} and the

19   righting behavior of individual sea urchins was recorded. I measured both the temperature at

20   which the animal could no longer right itself (T_{LoR}) and the righting time at temperatures below

21   the T_{LoR}. In all seasons, *D. antillarum* exhibited a higher mean T_{LoR} than *E. lucunter*. The mean

22   T_{LoR} of each species increased with increasing environmental temperature revealing that both

23   species acclimatize to seasonal changes in temperatures. The righting times of *D. antillarum*

24   were much shorter than those of *E. lucunter*. The longer relative spine length of *Diadema*

25   compared to that of *Echinometra* may contribute to their shorter righting times, but does not

26   explain their higher T_{LoR}. The thermal safety margin (the difference between the mean collection

27   temperature and the mean T_{LoR}) was between 3.07-3.66°C for *Echinometra* and 3.79-5.67°C for

28   *Diadema*. While these thermal safety margins exceed present day temperatures, they are modest

29   compared to those of temperate marine invertebrates. If sea temperatures increase more rapidly

30   than can be accommodated by the sea urchins (either by genetic adaptation, phenotypic

31   plasticity, or both), this will have important consequences for the structure of coral reefs.

33   **INTRODUCTION**

34   Adult sea urchins are grazers and have been dominant herbivores in many Caribbean reefs for

35   decades and perhaps millennia (Lessios, Garrido & Kessing, 2001; Levitan, Edmunds & Levitan,

36   2014). A convincing and well-documented example of their influence on coral reef community

37   structure occurred in the mid 1980's when Caribbean sea urchin populations of *Diadema*

38   *antillarum* experienced a massive die-off. The subsequent overgrowth of macroalgae resulted in

39   decreased coral cover and recruitment and concomitant biodiversity losses from which reefs have

40   not fully recovered (Jackson, 2001; Levitan, Edmunds & Levitan, 2014; Miller et al., 2009).

41   Nevertheless, rebounds in *Diadema* populations in certain Caribbean locations are correlated

42   with greater coral recruitment and coral growth (Edmunds & Carpenter, 2001; Knowlton, 2001;

43   Carpenter & Edmunds, 2006; Idjadi, Haring & Precht, 2010), which might presage an increase in

44   fish diversity (Rogers et al, 2014). The proximate cause of the *Diadema* die-off was likely a

45   disease agent that has never been identified (Beck, Miller & Ebersole, 2014), but additional

46   environmental stressors such as increasing ocean temperature due to global climate change may

47   also be deleterious for marine ectotherms such as echinoids particularly in intertidal and subtidal

48   tropical habitats (Nguyen et al. 2010).

49   Tropical sea temperatures are predicted to increase by as much as 4.8°C by the end of this

50   century (IPCC, 2014). Threshold temperatures for coral bleaching have been evaluated in light of

51   those predictions (e.g. Tolleter et al., 2013; Hoegh-Guldberg, 1999; Donner, 2011). There is also

52   a growing literature on the effects of anticipated future temperature increases on fertilization and

53   early development of echinoids (Brennand et al., 2010; Byrne, 2011; Byrne et al., 2009; Sewell

54   & Young, 1999). The few previous studies of thermal tolerance in adult sea urchins, however,

55   did not evaluate results in the context of global climate change (Lawrence, 1973; Lawrence &

56   Cowell, 1996; Ubaldo, Uy & Dy, 2007). Moreover, no thermal tolerance data exist for the

57   Caribbean keystone species, *Diadema antillarum.* Additionally, characterizing the thermal

58   tolerance of sea urchins might permit predictions about changes in their geographic ranges (Ling

59   et al., 2009).

60   I studied the thermal tolerance of the long-spined sea urchin, *Diadema antillarum,* and

61   compared it to the sympatric rock-boring sea urchin, *Echinometra lucunter,* which, unlike

62   *Diadema,* is not associated with low macroalgal cover (Furman & Heck, Jr., 2009). My study

63   site was in Grand Cayman, British West Indies, on the western side of the island within the

64   Marine Protected Area (McCoy, Dromard & Turner, 2009). I collected urchins from depths

65   ranging from just below the surface to 3 m. The animals were collected opportunistically based

66   on their accessibility and whether they would be too large to accommodate in the lab or too small

67   to be adults. Both species occurred at depths of 3 m, but only *Echinometra* occurred at the

68   shallowest depths; I never found *Diadema* less than about 30 cm below the water surface. I

69   would expect therefore that *Echinometra* might be exposed to higher daily temperatures than

70   *Diadema* and thus might have a higher thermal tolerance (Nguyen et al., 2011). On the other

71   hand, the rock boring behavior of *Echinometra* might mitigate temperature fluctuations given

72   that they were always wedged into crevices during the day, while I found *Diadema* in exposed

73   areas of the reef during the day.

74   I measured the thermal tolerance of individuals of these species over three seasons, and

75   thus three different temperature regimes to determine if they acclimatized to changes in

76   environmental water temperature. Finally, I measured variation in thermal tolerance among

77   individuals of the two species as such variation might serve as a substrate for natural selection in

78   warming seas.

79

80   **MATERIALS AND METHODS**

81   **Collection Site**

82   Sea urchins of both *Diadema antillarum* and *Echinometra lucunter* were collected (under a

83   permit granted by the Cayman Islands Department of Environment), by snorkeling in a small

84   rectangular inlet south of George Town harbour, Grand Cayman, located at 19°16'42.69" N,

85   81°23'34.79" W, (in the Marine Protected Area between study sites GCM9 and GCM5 of

86   McCoy, Dromard & Turner, 2009). The inlet was roughly 36 m long x 14 m wide with a gently

87   sloped floor that reached the more open sea at a depth of about 3 m. The walls of the inlet were

88   composed of eroded ironshore (Logan, 2013), with many cracks and crevices in which sea

89   urchins, particularly *E. lucunter*, were found (Fig 1a). The floor of the inlet was coral rubble and

90   sand where patches of *D. antillarum* were found (Fig. 1b).

91   Both species were collected in the afternoon during the winter (February, 2013), spring

92   (May, 2010) and summer (August, 2011) in order to assess the extent of acclimatization of

93   thermal tolerance among animals that had likely been exposed to substantial inter-seasonal

94   temperature variation. I measured the temperature at both shallow (10 cm below the surface) and

95   deeper collection sites (2.5 m below the surface) during each collection visit using a Fisher

96   Scientific Precision Thermometer, (accurate to 0.01°C) or a mercury thermometer (accurate to

97   0.1°C). Unexpectedly, there was no temperature difference with depth. I confirmed this by

98   collecting temperatures at 15-minute intervals for several days to a full week in both shallow and

99   deeper collection sites (Onset HOBO temperature probes and data logger). The shallow site was

100   not a sequestered intertidal pool but rather was flushed with seawater constantly, perhaps

101   accounting for the absence of a temperature differential between shallow and deeper sites.

102   Therefore, collection temperatures are reported as the combined mean from the shallow and deep

103   sites for each season.

104   **Animal maintenance in the laboratory**

105   Animals were maintained in a laboratory at the Cayman Islands Department of Environment

106   building in George Town, Grand Cayman. Between 4-8 sea urchins of either species were

107   maintained in a 50 l tank of aerated seawater at room temperature (22.5 ± 0.7°C) and under

108   natural light. All animals were tested within 3 days of collection. Animals were not fed while in

109   the laboratory.

110   **Measures of thermal tolerance: righting time and critical thermal maximum**

111   I measured both the righting time as temperature was increased and the temperature at which

112   each sea urchin could no longer right itself (T_{Lor}) after inversion as indicators of thermal

113   tolerance. The latter measurement is repeatable and indicates the temperature at which the

114   neuromuscular system of the animal no longer has sufficient integrity to mediate righting. It has

115 been a reliable indicator of stress in many animal species including echinoids (Lawrence &

116 Cowell, 1996; Challener & McClintock, 2013; Ubaldo, Uy & Dy, 2007).

117   Each sea urchin was tested individually and placed in a tank with a volume of room

118 temperature aerated seawater sufficient to cover the urchin and provide room for me to invert the

119 animal. The experimental substrate was smooth without sand or gravel. The water was aerated

120 through the entire experiment, which also mixed the water as it was heated. At the beginning of

121 each trial (in room temperature water), the sea urchin was placed on its aboral surface (using

122 wooden spatulas) and the time for the animal to right itself completely (its oral surface

123 contacting and parallel to the tank bottom) was recorded. The testing tanks were large and could

124 not be heated sufficiently using available heaters. In order to heat the water, therefore, small

125 volumes of test water were removed (without disturbing the test animal) and were replaced by

126 comparable volumes of aerated and heated water from a different tank (with a smaller volume

127 that was easier to heat). With practice following pilot studies, I was able to reliably increase the

128 water temperature in the test tank at a rate of 0.16-0.3 °C min^{-1}. I constantly mixed the water in

129 the test tank with a paddle and measured the water temperature with a Fisher Scientific Precision

130 Thermometer, (accurate to 0.01°C) which remained in the test tank. As the water was heated, the

131 animal was inverted periodically (roughly once for each degree increase, and more frequently as

132 loss of righting ability approached) and the righting time was recorded. The end point of the loss

133 of righting was taken as the temperature at which the animal no longer could right itself (within

134 15 minutes of inversion), and was designated the T_{LoR}. The animals were not dead at loss of

135 righting, as they continued to move their spines and mouthparts. Moreover, after the T_{LoR} was

136 noted, each animal was immediately placed in room temperature seawater after which

137 coordinated movement was restored. The sea urchins did not appear to habituate to inversion as

138 the righting times for an individual did not get progressively longer through the experiment until

139 T_{LoR} was imminent.

140   In order to determine if age (size) influenced the T_{LoR}, I measured the test diameter of

141 each sea urchin following the experiment with vernier calipers (to the nearest mm). If the test

142 shape of the sea urchin was not a circle, I measured the major axis. *D. antillarum* have spines of

143 very different length while those of *E. lucunter* are more similar in length and this difference in

144 morphology appeared to affect how the animals maneuvered themselves during righting.

145 Therefore, I also measured the length of a spine that appeared to be among the longest on each

146 animal.

147   In other studies (e.g. Lawrence, 1973), inverted animals were placed in water of

148 particular temperatures and then righting time was measured, whereas in this study, the water

149 was heated until the animal could no longer right itself. Heating rates affect the thermal tolerance

150 of many marine invertebrates (Nguyen et al., 2011). The data in the present study reflect acute

151 responses to increasing temperatures of animals taken from the wild that had been acclimatized

152 to winter, spring, or summer temperatures.

153   The mean collection temperatures (±SEM) were 27.2°C (±0.12) in February, 28.8°C

154 (±0.13) in May, and 30.4°C (±0.09). In Figure 2, I compared the mean collection temperatures of

155 this study with data from the Cayman Islands provided by the National Oceanic and Atmospheric

156 Administration (NOAA) Coral Reef Watch (2000, sampled twice weekly). I used NOAA data

157 from 2010-2013 in the months of February, May and August to determine if my collection

158 temperatures were representative of typical seasonal Cayman Islands reef water temperatures. In

159 both data sets, there are comparable changes in mean temperatures with season. Moreover, the

160 temperatures I measured are consistent with those reported in the NOAA data albeit slightly

161 higher by 0.58-0.8°C. I collected temperatures during the day while the NOAA data were

162 collected at night, accounting for the slightly greater temperatures reported here (Fig. 2).

163 **Statistical analyses**

164 To determine if there were differences between species and among collection temperatures in

165 loss of righting temperatures (T_{LoR}), I performed a two-way ANOVA with species and collection

166 temperatures as fixed factors and T_{LoR} as the dependent variable. At temperatures below the T_{LoR}

167 (≤ 30.9°C) I analyzed whether species and collection temperatures affected righting times using a

168 multiple regression analysis. I also compared the ratio of the length of a long spine to test

169 diameter between the two species using the Student's t-test. Finally, I performed linear

170 regression analyses to determine if size (test diameter) was a predictor of T_{LoR} for each species in

171 each season.

172

173 **RESULTS**

174 The mean temperatures for loss of righting (T_{LoR}) of both species were greater than the collection

175 temperatures and increased with increasing collection temperature, so that those collected in the

176 winter had the lowest thermal tolerance and the summer collected sea urchins had the highest

177 (Fig. 3). *D. antillarum* lost righting ability at significantly higher temperatures than *E. lucunter*

178 at all collection temperatures (Fig. 3). The 2-way ANOVA showed that both species (p<0.0001)

179 and collection temperature (p<0.0001) were significant predictors of T_{LoR} but their interaction

180 was not (p=0.12). The difference between the mean collection temperature and the mean T_{LoR},

181 which can be thought of as the thermal safety margin (Nguyen et al., 2011), was more than 3°C

182 for *E. lucunter* in all seasons (Table 1). The thermal safety margin of *D. antillarum* was almost

183 6°C in winter and summer but only 3.79°C in the spring. Thus, the T_{LoR} of *E. lucunter* increased

184   roughly linearly with seasonal temperature. However, the T_{LoR} of *D. antillarum*, while greater

185   than that of *E. lucunter*, did not change from winter to spring, although it was higher in the

186   summer (Fig. 3; Table 1).

187   There was variation in T_{LoR} within both species (Table 2). *Diadema* exhibited the largest

188   range in T_{LoR} during the winter (5.3°C) while *Echinometra* exhibited the largest range in T_{LoR}

189   during the summer (3.6°C).

190   The rock boring *E. lucunter* took longer to right themselves compared to *D. antillarum* at

191   all temperatures below the T_{LoR} ($p<0.0001$; Fig. 4). Collection temperature also affected the

192   righting times below the T_{LoR} ($p=0.025$), likely due to the slower righting times of winter

193   collected *Diadema*. The temperature at which the sea urchins were tested did not have a

194   significant effect on righting times ($p=0.561$). Typically, the *E. lucunter* that righted themselves

195   took between 100-240 seconds while *D. antillarum* righted themselves in less than 100 seconds.

196   I have provided video examples of the righting behavior of both species in the supplementary

197   material.

198   When the long-spined sea urchin righted itself, it appeared to rely on the levering action

199   of the longer spines, which exceeded the diameter of the test, to rock the animal onto its side.

200   The rock boring sea urchin, on the other hand, used its tube feet rather than its spines, which

201   were shorter than the test diameter, to push and pull itself onto its side. The greater mean ratio of

202   the length of a spine to test diameter in *Diadema* (1.38 ±0.1) compared to *Echinometra* (0.78 ±

203   0.04) is illustrated in Figure 5 ($p<0.0001$).

204   T_{LoR} did not vary with test diameter in either species (Fig. 6; for *D. antillarum*, p values

205   for all seasons >0.4; for *E. lucunter*, p values for all seasons >0.1). Although the test diameters

206   overlapped between the two species, on average, *Diadema* were larger than *Echinometra*.

207

208   **DISCUSSION**

209   Temperature affects the physiological responses of tropical marine animals more than other

210   possible stressors of climate change (Przeslawski et al., 2008). Both species of sea urchin in this

211   study exhibited acclimatization to seasonal temperature changes in experiments measuring acute

212   thermal tolerance (Fig. 3), their T_{LoR} increasing with increases in environmental temperature.

213   Nevertheless, like other tropical animals, the safety margin of thermal tolerance above ambient

214   temperatures (~ 3-6°C, Table 1) was small compared to that of temperate animals (Przeslawski et

215   al., 2008; Nguyen et al 2011). It is possible that the thermal safety margins of the sea urchins

216   would be different with a slower rather than acute temperature increase that would more closely

217   resemble natural temperature changes. However, Nguyen et al. (2011) demonstrated that

218   subtidal tropical animals exhibited lower thermal tolerances when heated at slower rates. So the

219   thermal tolerances reported in this study likely represent the highest tolerances that these animals

220   can exhibit given how rapidly they were heated. Nevertheless, different thermal tolerance end

221   points and different heating rates (e.g. Hernández et al, 2004; Nguyen et al, 2011) make

222   comparisons of particular thermal tolerances across different studies difficult.

223   *Diadema* exhibited the largest range in T_{LoR} during the winter and the smallest range

224   during the summer, while *Echinometra* showed the opposite tendency, with the largest range in

225   T_{LoR} in the summer (Table 2). These variations in thermal tolerance suggest some capacity for

226   evolutionary adaptation to temperature changes if the variation among adults has a genetic

227   component. The sea urchins also exhibited variation in righting times at temperatures below the

228   T_{LoR} (Fig. 4) and this variation may affect their daily movements such as foraging, in warming

229   seas. Like other benthic invertebrates, sea urchins have pelagic larvae, which may be exposed to

230   different conditions from those of adults. Since larvae disperse widely (Lessios, 1988), urchins

231   have the potential to establish in new areas, facilitating range changes in response to global

232   climate change (Ling et al, 2009; Przeslawski et al., 2008). Alternatively, if sea urchins cannot

233   adapt to the rapid changes in their environments, local populations may become extinct.

234   The proximate causes of interspecific differences in thermal tolerance responses are

235   unclear (Fig. 3 and Fig. 4). Both species were exposed to similar daily and seasonal temperature

236   variations. One possible proximate cause of the faster righting time of *Diadema* is the difference

237   in spine length relative to test size (Fig. 5). The *Diadema* used their relatively long aboral spines

238   as levers to topple them over when righting. The *Echinometra*, having much shorter spines, used

239   their tube feet to right themselves, which was a more time consuming process. The different

240   uses of spines versus tube feet have been reported in other motor behaviors of sea urchins as well

241   by Domenici, González-Calderón, & Ferrari (2003). They, however, found that size affected

242   motor behavior on vertical and horizontal surfaces, whereas size had no effect on righting

243   behavior in my study (Fig. 6), nor did it affect thermal safety margins in other tropical

244   ectotherms (Nguyen et al, 2011). The different relative length of spines might explain why

245   *Echinometra* took longer to right themselves at temperatures below T_{LoR}. However, it would not

246   account for the lower T_{LoR} (Fig. 3) and smaller thermal safety margin (Table 1) of *Echinometra*.

247   Righting behavior may have more survival value to *Diadema* than *Echinometra.* Both species

248   forage at night (Hendler et al., 1995) but only *Diadema* were found in the open during the day

249   and I have observed fish flipping them over in order to eat them. The rock-boring urchins, on the

250   other hand, as the name implies, are jammed into crevices and typically not found in the open

251   during the day. At night, the temperature can fall by as much as 1°C in the summer (unpublished

252   data) so *Echinometra* are less likely to be exposed and vulnerable during higher daytime

253   temperatures.

254   Phase shifts from coral to macroalgal dominance following the *Diadema antillarum* die

255   off in the Caribbean have been widely reported (e.g. Jackson, 2001, Lessios, 1988). There

256   appears to be great regional variation in the recovery of different populations of these sea urchins

257   (Carpenter & Edmunds, 2006; Levitan, Edmunds & Levitan, 2014; Miller et al., 2009). Regions

258   in which *Diadema* are increasing in number are correlated with increases in coral settling and

259   cover (Carpenter & Edmunds, 2006; Knowlton, 2001; Furman & Heck, Jr. 2009; Idjadi, Haring

260   & Precht, 2010). Unlike *D. antillarum* populations, *E. lucunter* populations have been relatively

261   stable throughout the Caribbean and have not been associated with changes in coral density

262   (Furman & Heck, Jr., 2009). Both species of sea urchins in the present study were collected

263   from local populations in a small area in a Grand Cayman reef. It is not clear, therefore, how

264   representative their thermal tolerance responses are compared to sea urchins from other areas.

265   Both species demonstrated a significant capacity to acclimatize to different seasonal

266   temperatures, which may serve them well as sea temperatures increase. Nguyen et al. (2011)

267   suggested that temperature increases as low as 2-3°C above present levels are likely to be

268   stressful to tropical marine ectotherms. The sea urchins in this study, however, appear to be able

269   to tolerate such changes. Additional studies are required to determine the capacity of sea urchins

270   to adapt to acute versus long-term thermal stress and the costs of such adaptation as global sea

271   temperatures increase**.**

272

273   **CONCLUSION**

274 Tropical sea temperatures may increase by as much as 4.8°C by the end of this century (IPCC,

275 2014). It remains to be seen if sea urchins will be able to adapt to these higher temperatures.

276 Moreover, other stressors (such as ocean acidification, infectious disease, runoff from land) are

277 likely to have synergistically deleterious effects on tropical marine ectotherms (Przeslawski et

278 al., 2008). Populations may adapt to higher sea temperatures by natural selection given the

279 within season variation in thermal tolerance exhibited by sea urchins in this study. The sea

280 urchins revealed at least seasonal plasticity in their capacity to acclimatize to different

281 temperatures. Alternatively, if sea temperatures increase more rapidly than can be

282 accommodated by sea urchins, local populations may become extinct. Changes in the number of

283 *Diadema antillarum*, in particular, will have important consequences for the structure of coral

284 reefs.

285

286 **ADDITIONAL INFORMATION AND DECLARATIONS**

287 **Competing interests**

288 The author declares there are no competing interests.

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291 **Author contributions**

292 The author conceived, designed, conducted the experiments, analyzed the results, and prepared

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305   **Supplemental information**

306   Videos of righting behavior (at 2x normal speed) in *Diadema antillarum* and *Echinometra*

307   *lucunter.*

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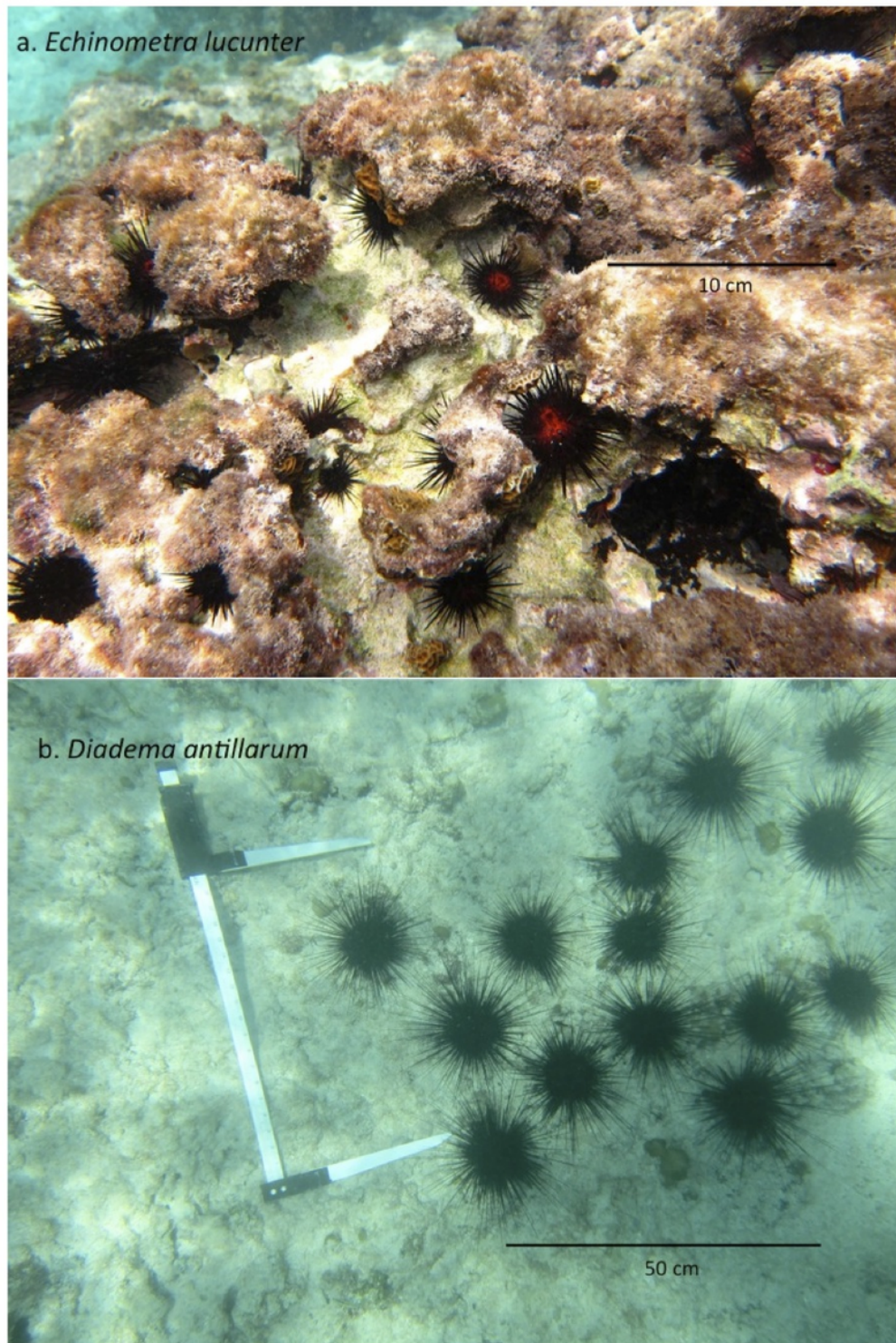
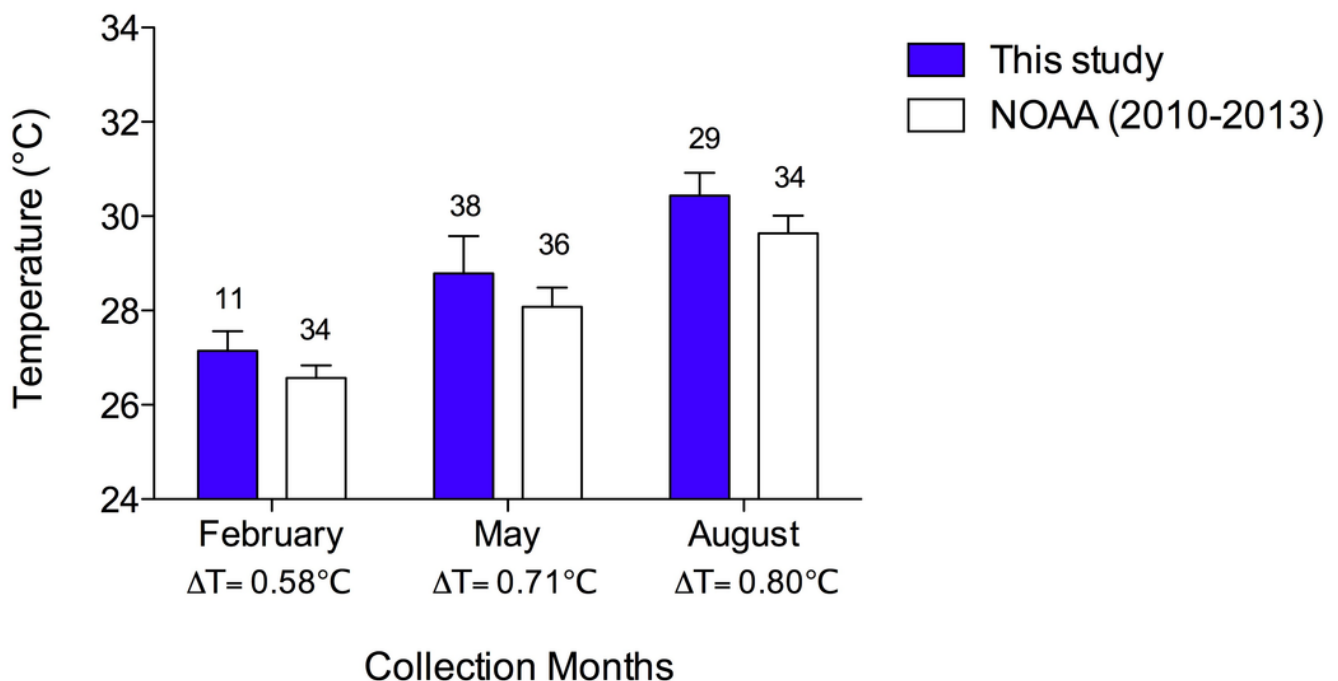
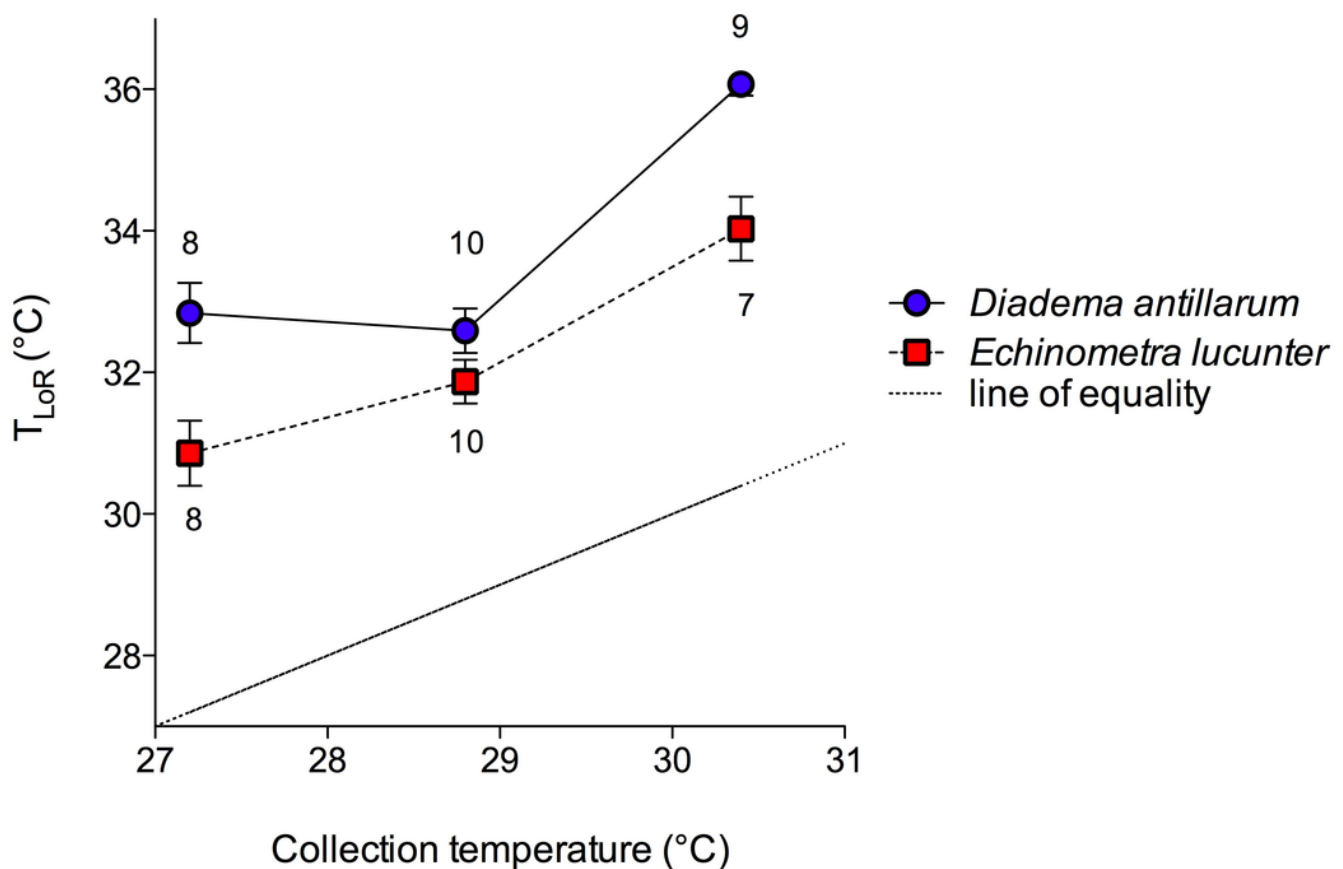
Sea urchins in field sites.

Sea urchins in field sites. A) *Echinometra lucunter.* B) *Diadema antillarum.*

2

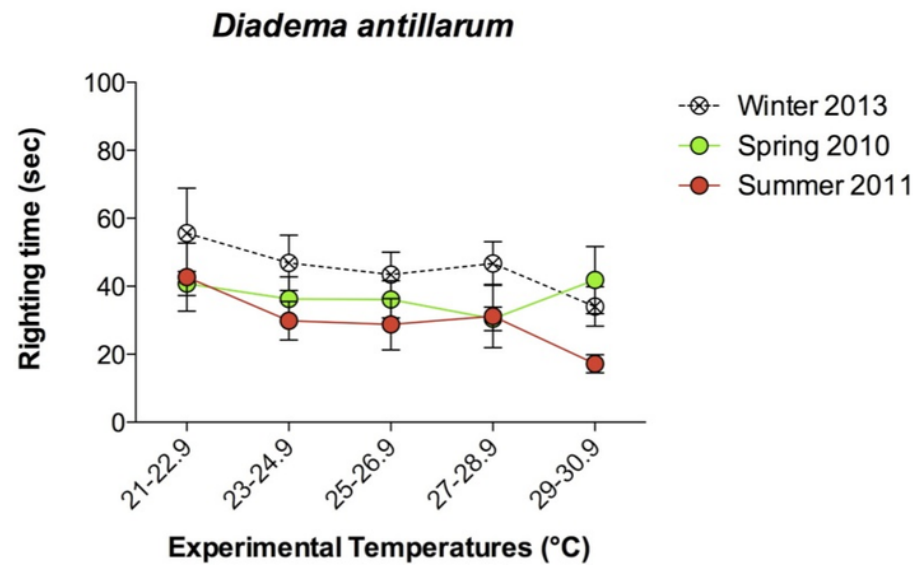
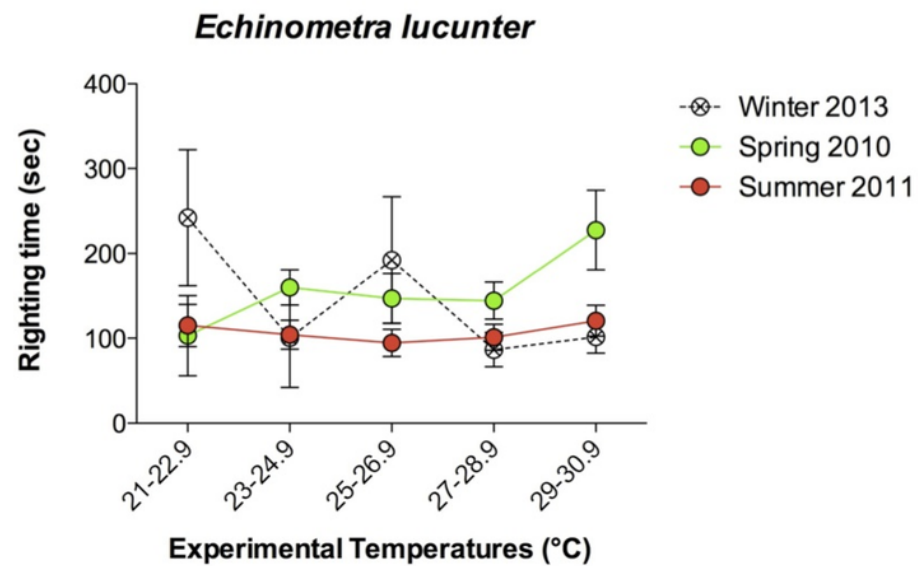
Sea temperatures.

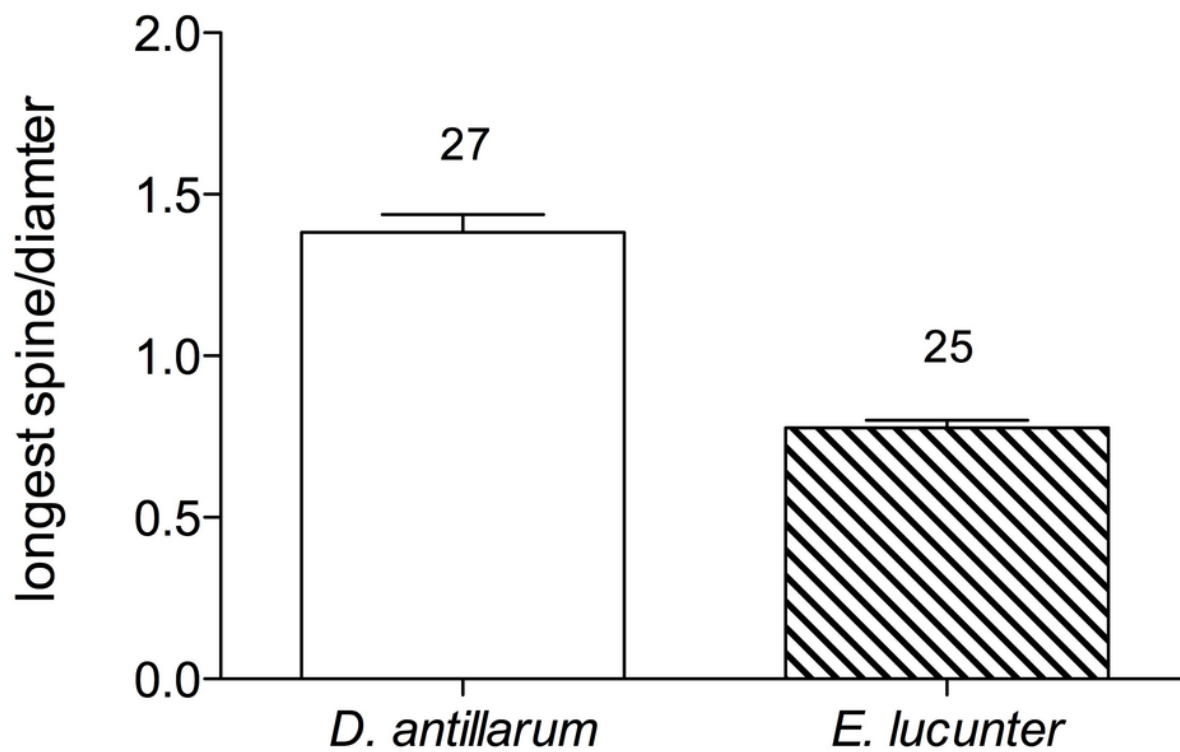
Sea temperatures reported in this study compared to reef sea temperatures of the Cayman Islands in February, May, and August, 2010-2013, reported by NOAA Coral Reef Watch. Bars represent means with vertical lines representing 1 SEM. Sample sizes are indicated above bars. The difference between mean temperature in this study and that of NOAA data are indicated by a Δ below the x-axis. A two-way ANOVA revealed that temperatures increased with month ($p<0.0001$) in both data sets and that the NOAA data (recorded at night) were significantly lower than the data from the present study, which were recorded during the day ($p<0.0001$). There was no interaction of temperature and study ($p=0.541$).

Temperature at the loss of righting (T$_{LoR}$)

Temperature at the loss of righting (T$_{LoR}$) of *D. antillarum* and *E. lucunter* at different collection temperatures. The symbols represent mean **T$_{LoR}$** with vertical lines representing 1 SEM. Sample sizes are indicated above or below the symbol. The dotted line represents the line of equality, **T$_{LoR}$** =sea temperature. The thermal safety margin is the distance between the fitted lines and the line of equality. The main effects of species ($F_{1, 46}$ = 29.51, p<0.0001) and collection temperature ($F_{2, 46}$ = 48.17, p<0.0001) were significant predictors of T$_{LoR}$ but their interaction was not ($F_{2, 46}$ = 2.189, p=0.12).

Mean righting times (±SEM) at increasing experimental temperatures (below T_{LoR})

Mean righting times (±SEM) at increasing experimental temperatures (below T_{LoR}) of A) *Diadema* and B) *Echinometra* collected during the winter, spring, and summer. For clarity, the data are displayed in bins of experimental temperatures of 1.9°C. Species ($p<0.0001$) and collection temperature ($p=0.025$) significantly affected righting time but the temperatures at which the sea urchins were tested did not ($p=0.561$). Model: $F_{3,431} = 56.58$; $p<0.0001$; $R^2 = 0.28$. Note that the y-axes are scaled differently.

A.

B.

Mean ratio of longest spine per test diameter

Mean ratio of longest spine per test diameter (±SEM) of *Diadema* and *Echinometra* (t=10.74, df=51; p<0.0001). Sample sizes are indicated above the bars.

T_{LoR} as a function of test size

$T_{\textbf{LoR}}$ as a function of test size in A) *Diadema* and B) *Echinometra* collected in the winter, spring, and summer. None of the slopes is significantly different from 0. *Diadema*: $p_{winter} =$ 0.396; $p_{spring} = 0.528$; $p_{summer} = 0.818$. *Echinometra*: $p_{winter} = 0.783$; $p_{spring} = 0.689$ $p_{summer} = 0.10$. Note that the x-axes are scaled differently.

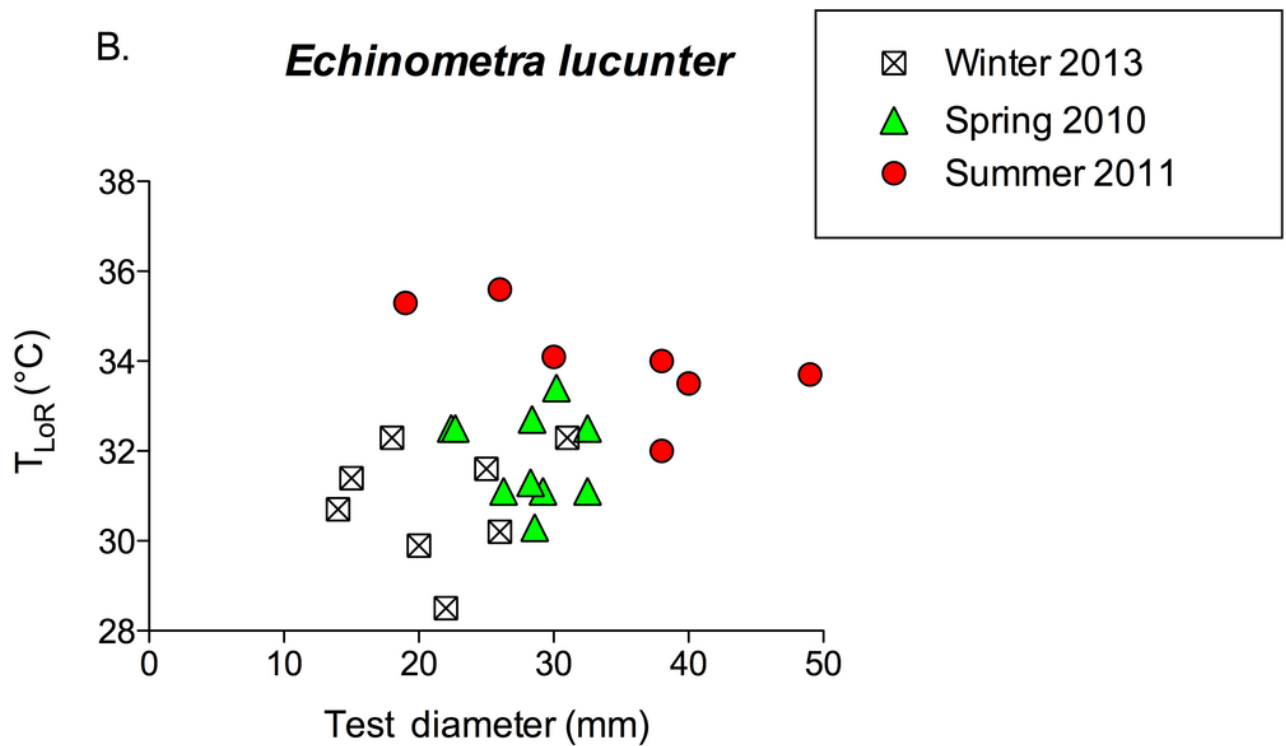
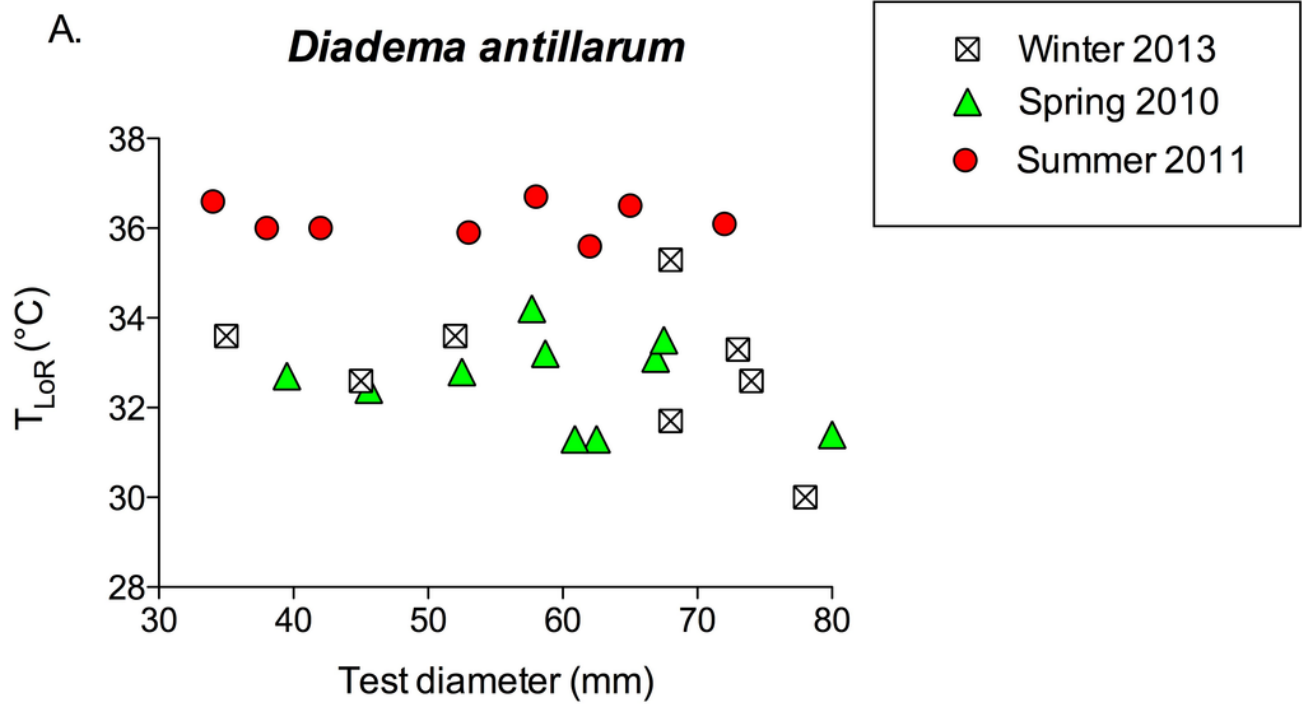



Table 1

Difference between mean T_{LoR} and mean collection temperature (thermal safety margin) for both species.

	D. antillarum	*E. lucunter*
FEBRUARY	5.64°C	3.66°C
MAY	3.79°C	3.07°C
AUGUST	5.67°C	3.63°C

Table 2

Ranges in T_{LoR} of both species across the 3 collecting seasons. Numbers in parentheses represent the difference between the highest and lowest T_{LoR} for each species.

	D. antillarum	*E. lucunter*
FEBRUARY	30.0-35.3°C (5.3)	29.9-32.3°C (2.4)
MAY	31.3-34.2°C (2.9)	30.3-33.4°C (3.1)
AUGUST	35.2-36.7°C (1.5)	32.0-35.6°C (3.6)